A gravel beach shelled micro-gastropod assemblage from Ceuta, Strait of Gibraltar, with the description of a new truncatelloidean genus

by Winston F. PONDER

Abstract. — An interstitial shelled gastropod assemblage from an intertidal gravel beach at Ceuta, southern Strait of Gibraltar, is described. Apart from a juvenile trochid (*Gibbula racketti*), the fauna of minute gastropods is dominated by six species forming three morphologically similar species pairs. There are two species of Skeneidae and Caecidae, together with two species previously included in the rissoid genus *Peringiella*. Each species pair is convergent in shell morphology, the *Peringiella*-like species are shown to belong in different families. One, *P. elegans*, is a rissoid but the other, *P. epidaurica*, is shown to be a new genus, *Botryphallus*, which is provisionally included in the Hydrobiidae (Littoridininae). The vertical distribution of this fauna on the beach is briefly described.

Résumé. — L'auteur décrit une faunule interstitielle de gastéropodes testacés d'une plage de graviers intertidale à Ceuta, sur la rive africaine du détroit de Gibraltar. A part de jeunes Trochidae (*Gibbula racketti*), cette faune de microgastéropodes est dominée par 6 espèces constituant trois paires d'espèces morphologiquement proches : deux Skeneidae, deux Caecidae, et deux espèces jusqu'ici classées dans le genre *Peringiella* (Rissoidae). Les espèces de chaque paire convergent pour la morphologie de la coquille, et il est montré que les espèces à coquille de type *Peringiella* appartiennent à des familles différentes. L'une, *P. elegans*, est bien un Rissoidae, tandis que pour *P. epidaurica* est créé le nouveau genre *Botryphallus*, classé provisoirement dans les Hydrobiidae Littoridininae. La microdistribution verticale de cette faunule est sommairement décrite.

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INTRODUCTION

During a workshop in 1986 at Ceuta, on the north African side of the Strait of Gibraltar (see fig. 1 for location), a gravel beach interstitial molluscan fauna was revealed during general collecting. As there are few records of such a fauna on gravel shores an attempt was made, in the one tide available to do the work, to crudely quantify its intertidal distribution. The general topography and sediments on the beach chosen for this more detailed work are shown in figure 2. In addition the opportunity is taken to revise the taxonomic position of three of the animals dominating this assemblage.

METHODS

Material was collected along two transects at Sarchal Bay, Ceuta (figs 1, 2 and table 1) on the same day (13.5.1986) in the main part of the beach. The profile of the shore at each
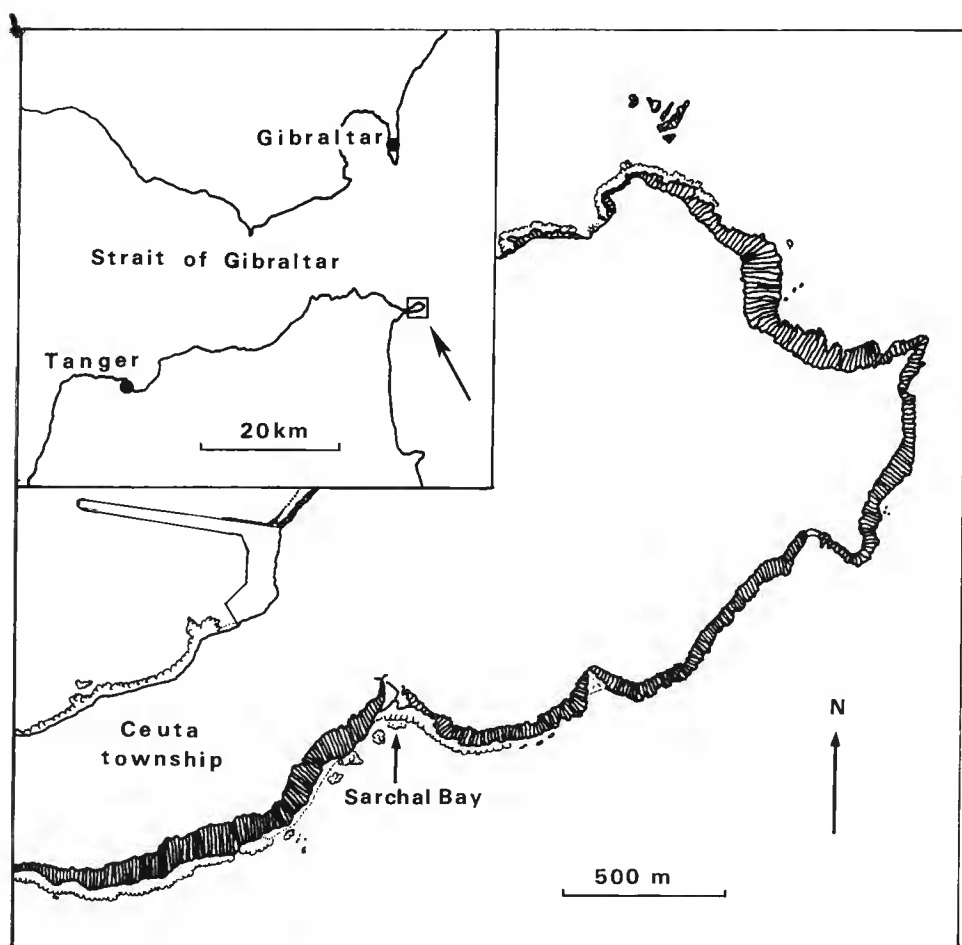
Fig. 1. — Map of Ceuta showing the location of Sarchal Bay.

transect was sketched and the general topography and gross aspects of the sediment noted. Distances between samples (stations) were estimated by pacing and, although these distances are given in metres below they are to be taken as only approximate indications.

The two transects were approximately 15 m apart and the horizontal distance between low tide spring (LTS) and high tide spring (HTS) was estimated to be about 14 m. The distance from high tide spring (the top of the beach slope) to the base of the cliffs was about 9-10 m. The main slope of the middle and upper shore was estimated to be about 1.3-1.4 m. The approximate distances down the slope from HTS for each sample site were as follows (see table 1 for other details) : — 1, 0 m, 2, 2.5 m, 3, 6.5 m, 4, 7.8 m, 5, 9.5 m 6, 14 m. The equivalent stations on the two transects were also at approximately the same vertical height on the shore. The main difference between the two transects was that the gravel in transect 2 was more
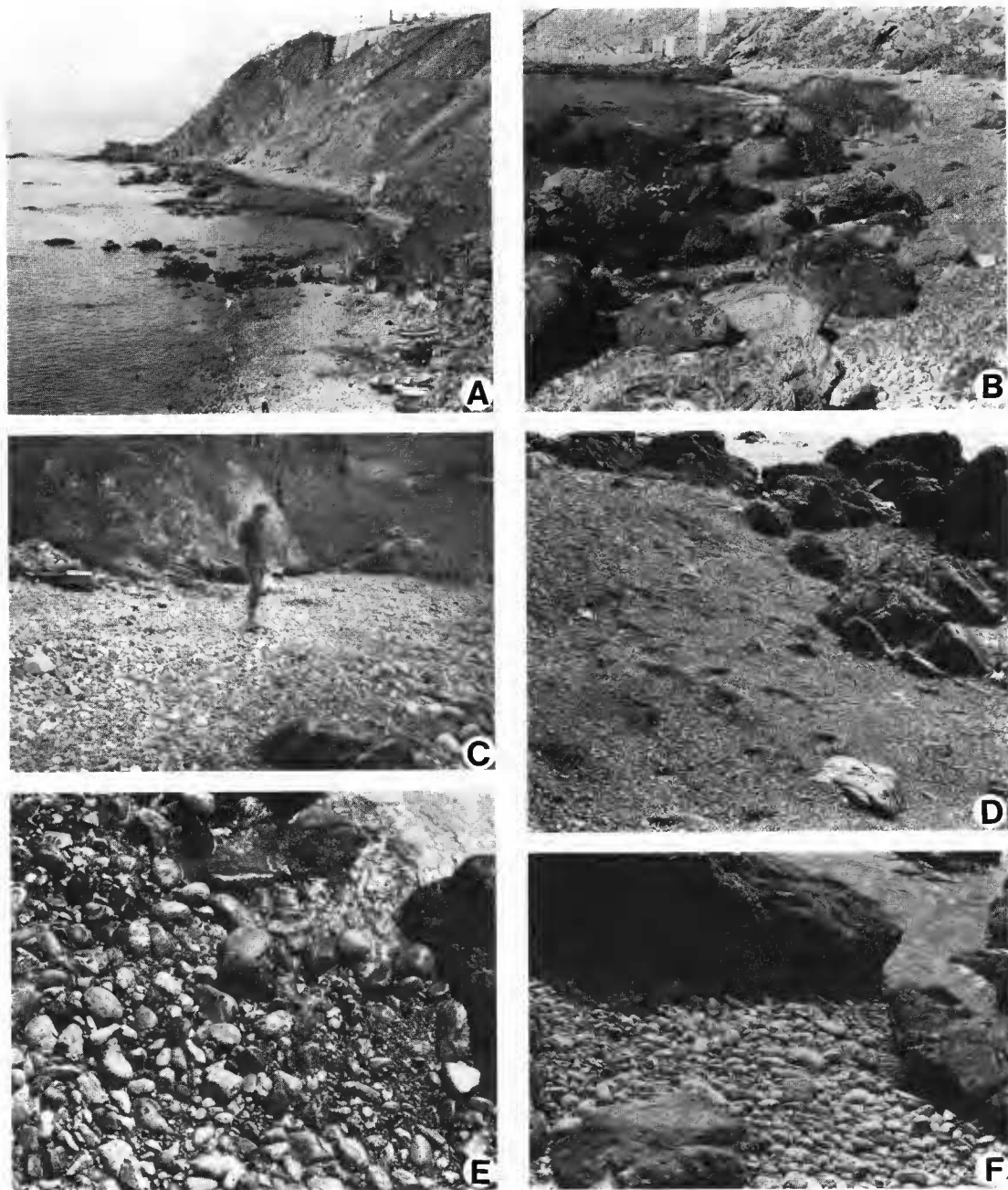
FIG. 2. — A-F. Sarchal Bay, Ceuta : A, general view of the beach; B, the area where the transects were made; C, the supralittoral part of the beach (from high tide spring); D, high tide spring and the steep slope immediately below — the preferred habitat of *Botryphallus epidauricus* (Brusina); E, F, the lower shore (at about low tide neap).

stable, especially in the upper part of the shore and there were more and larger blocks of rock, although rock outcrops also occurred on transect 1 (table 1).

Sufficient gravel was dug by hand from each station to fill a four litre (.004 m³) plastic container. In the upper parts of the beach the dry top layer was removed, and the damp gravel below was sampled down to a maximum depth of approx. 15 cms. A lower sandy layer was present in some of the stations and this was regarded as the maximum depth when present (i.e. the sand was not collected). Material from the two lowest stations on each transect, and the third lowest on transect 1, was collected under water so that some washing must have occurred, causing some reduction in the numbers of animals in those samples. The gravel was then washed in a bucket of seawater through a sieve with 2 mm mesh. The residue passing through the sieve was preserved in 10 % seawater formalin and later sorted and individuals counted. Replicate samples were not obtained at each station because of time constraints. Because of the lack of replicates, and because of the problems with washing as the lowest samples were collected, the numbers obtained cannot be treated as a valid quantitative estimates and consequently are not listed as such. The numbers obtained are, however, outlined to provide a general picture of abundance and distribution.

Living specimens of the two *Peringiella* species were examined. They were also dissected after fixation in 10 % seawater formalin. Four to five Bouins fixed specimens of these two species were sectioned at 4 and 6 μm after embedding in paraplast and were stained with Mallory's triple stain and Ehrlich's haematoxylin and eosin.   .

The bulk of the material used in this study is housed in the Muséum national d'Histoire naturelle, Paris (MNHN) and voucher specimens have been lodged in the Australian Museum, Sydney (AMS).

TABLE 1. — A brief description of the stations on the two transects. HTS — high tide spring; LTN — low tide neap; LTS — low tide spring.

Transect 1

1 — Coarse to medium gravel, very few small cobbles, near top of upper beach slope. Near small rock. Very low stability. No shade (equivalent to HTS).

2 — Gravel with about 40 % cobbles, near base of upper beach slope. Near small rock which provides some shade.

3 — Similar to last but lower, with *Melaraphe neritoides, Siphonaria* and *Patella* common on rocks at this level. Some shade amongst rocks.

4 — Coarse + fine gravel with about 40 % cobbles amongst boulders at base of beach slope, at upper edge of boulders covered with green algae. Approx. low neap tide level (LTN). Sample collected in water.

5 — Gravel, in middle of green algae-covered boulder area taken in c. 15-20 cm water depth at LTN.

6 — As last but further out and at about 25-35 cm water depth at LTN (approx. equal to LTS level).

Transect 2

1 — Gravel with about 20 % small cobbles and some coarse sand just below upper edge of beach slope. At upper side of large rock in wide crevice between two rocks. Little stability. Very little shade (equivalent to HTS).

2 — About equal amounts of gravel and cobbles, little coarse sand. In and near crevice between two large rocks. Moderate stability. Some shade.

3 — Cobbles (about 40 %), gravel and coarse sand. On edge of large rock. Some shade. Little stability.

4 — Gravel and coarse sand with large cobbles amongst large rocks. Medium stability. Approx. equal to LTN. Just below upper edge of green algal zone at base of beach slope. Sample collected in water.

5 — No equivalent sample taken.

6 — Rust-coloured gravel beneath and between boulders in about 25-35 cm water depth at c. LTN (approx. equal to about LTS).

RESULTS

I — THE FAUNA

In this section the dominant elements of the fauna are listed and discussed. The following species occurred in low numbers (< 5 in any sample) and will not be discussed further : *Scissurella* sp., *Tricolia* sp., *Nodulus contortus* (Jeffreys, 1856), *Pisinna punctulum* (Philippi, 1836), *Rissoella* sp., and *Lasaea rubra* (Montagu, 1803).

The taxonomy of most of the species listed below generally follows that of VAN AARTSEN *et al.* (1984).

Family SKENEIDAE

Two species of Skeneidae were abundant and were identified by S. GOFAS. These names are used somewhat tentatively given the state of the taxonomy of this group. I have illustrated the shells (including the protoconch), opercula and radulae to facilitate future recognition.

Skenea serpuloides (Montagu, 1808)
(Figs 3F-I, 4D-F)

Adult shells of this species range from about 1.1 to 1.25 mm in diameter and 0.6-0.7 mm in height. The radula (fig. 4E, F) and operculum (fig. 4D) is illustrated for comparison with the next species. The radula has four lateral teeth, the inner three bearing sharp cusps the outermost with a single weak cusp. The central teeth have a few (usually 3) weak cusps.

Dikoleps pruinosa (Chaster, 1896)
(Figs 3A-E, 4A-C)

Adult shells (fig. 3A-D) range from about 0.9 to 1.0 mm in diameter and 0.6-0.8 mm in height. They differ from the first species in having a thinner, more globose shell, a sinuate outer lip (also reflected in the sharp axial growth lines — see especially fig. 3C), fewer coils in the operculum (fig. 4A) and the radula (fig. 4B, C) has four non-cuspate lateral teeth, the outermost similar in form to that of *S. serpuloides*. The differences in the radula were the basis for the generic separation of this group of species from *Skenea* (Höisaeter, 1968). Specimens of
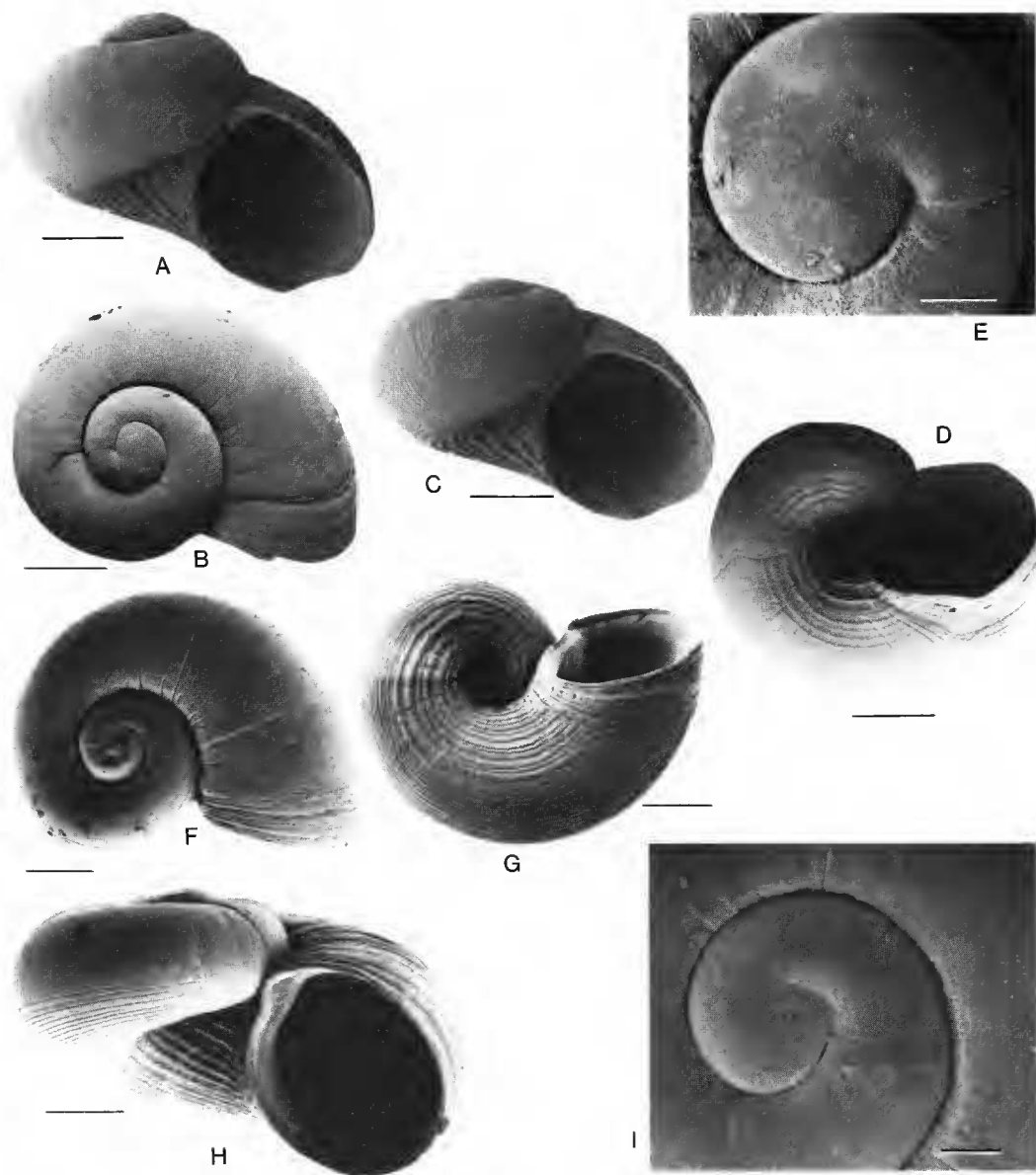
FIG. 3 — Shells of Skeneidae : A-E, *Dikoleps pruinosa* (Chaster) ; E, protoconch. F-I, *Skenea serpuloides* (Montagu) ; I, protoconch.
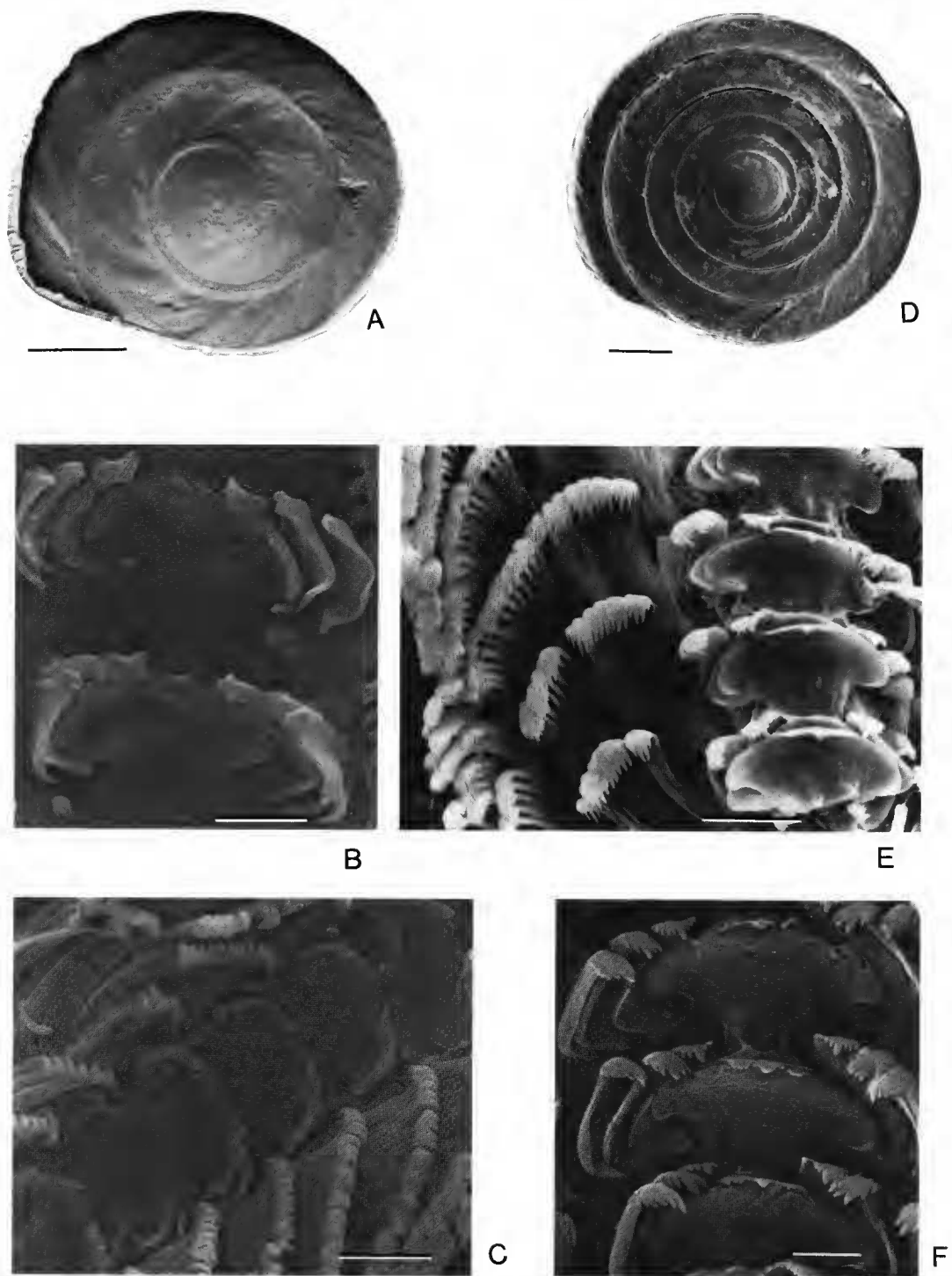Scales : A-D, F-H = 0.25 mm ; E, I = 50 μm.

FIG. 4. — Opercula and radulae of Skeneidae : A-C, *Dikoleps pruinosa* (Chaster) : A, operculum ; B, C, radula, B, detail of central and lateral teeth. D-F, *Skenea serpuloides* (Montagu) : D, operculum ; E, F, radula, F, detail of central and lateral teeth.

Scales : A-D = 0.1 mm; B, F = 5 μm; C, E = 10 μm.

this species vary in the strength of the axial growth lines (compare fig. 3A and C). *Dikoleps nitens* (Philippi, 1844) is, perhaps, a smooth form of this species.

Family TROCHIDAE

Gibbula racketti (Payraudeau, 1826)

Juvenile (< 2 mm in diam.) of this species were surprisingly abundant in the gravel and are presumably a seasonal phenomenon. Such a habitat for juveniles of this species is somewhat unexpected.

Family CAECIDAE

The classification of Mediterranean Caecidae has been reviewed by VAN AARTSEN (1977) and PANETTA (1980).

Caecum incomptum Monterosato, 1884
(Fig 5G, H)

This taxon is regarded as a variety of *C. auriculatum* Folin, 1868 by VAN AARTSEN (1977) and VAN AARTSEN *et al.* (1984) and a synonym of that species by PANETTA (1980). The specimens collected in this study are all the taxon referred to the *C. incomptum* "form" by VAN AARTSEN (1977), showing the characteristic dome-shaped septum and lacking any axial rings or apertural swelling. There seems to be justification for recognition of this taxon as a separate species whose relationships appear to be with *C. glabrum* (Montagu, 1803) rather than with *C. auriculatum*, given the shape of the septum and the lack of an apertural ring. VAN AARTSEN (1977) did not examine type material and, as far as I can determine, type material has not been figured. As the name *incomptum* has been used for this taxon I continue to use the name, although its validity needs to be confirmed.

Caecum incomptum is very abundant in the intertidal gravel habitat and can be distinguished from the next species by the evenly rounded septum. Shells of this species reach about 1.6 mm in length.

Caecum clarkii Carpenter, 1858
(Fig. 5I, J)

This species has an oblique, pointed septum but otherwise closely resembles the last species. Adult shells reach about 2.1 mm in length and there is a faint longitudinal (i.e. spiral) sculpture on the shell.
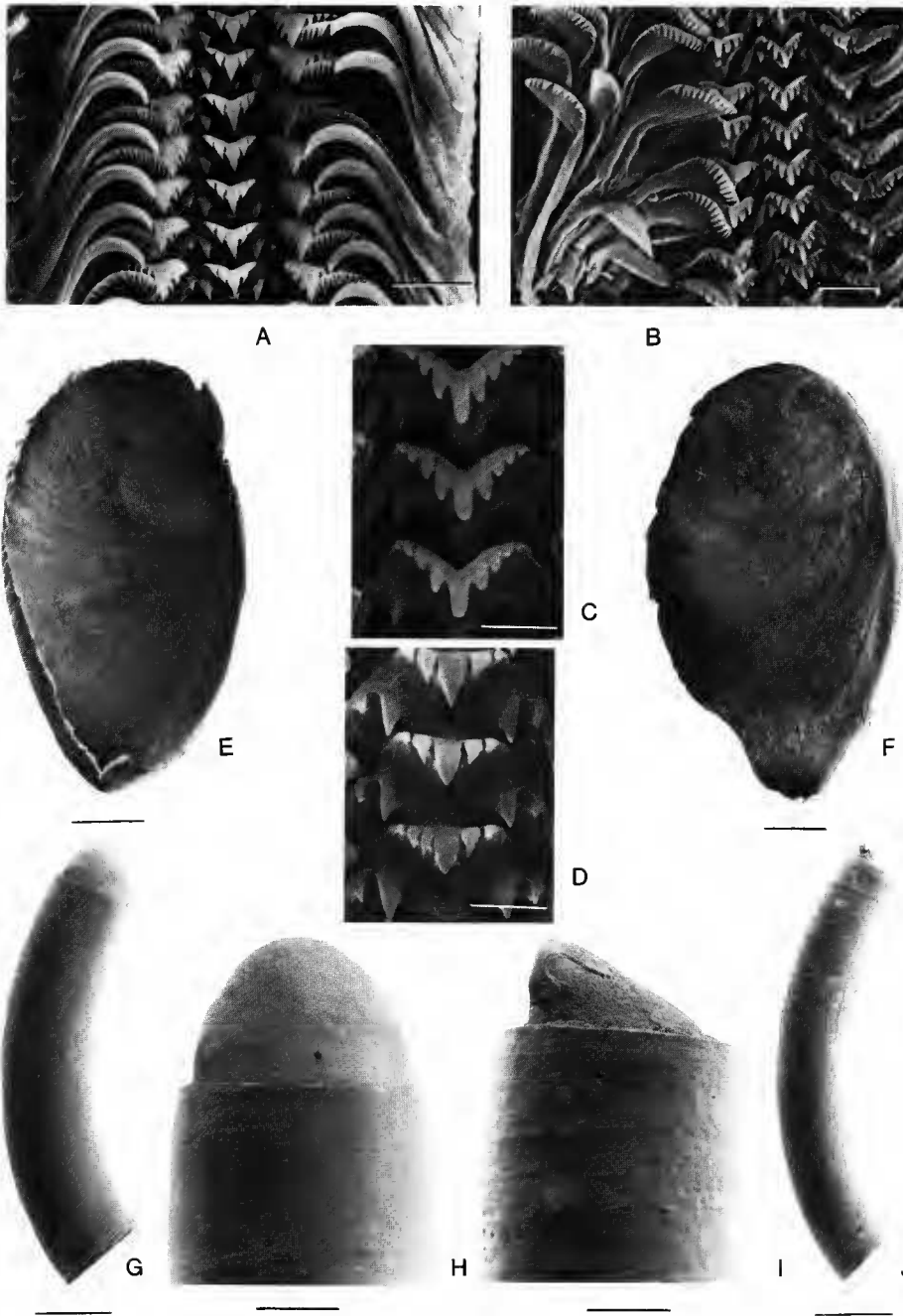
FIG. 5. — A, D, E, radula (A, D) and operculum (E) of *Peringiella elegans* (Locard); D, detail of central teeth. B, C, F, radula and operculum of *Botryphallus epidauricus* (Brusina); C, detail of central teeth. G, H, *Caecum incomptum* (Monterosato); H, detail of septum. I, J, *Caecum clarkii* (Carpenter); I, détail of septum.
Scales : A = 10 μm; B, D = 5 μm; C = 2.5 μm; E, H, I = 0.1 mm; F = 50 μm; G, J = 0.3 mm.

Family RISSOIDAE

Genus **PERINGIELLA** Monterosato, 1878

TYPE SPECIES : *Peringiella denticulata* Ponder, 1985, new name for *Rissoa laevis* Monterosato, 1877 (non Sowerby, 1829).

The two species described below have usually been included in *Peringiella*, but the type species of that genus is not known anatomically and has denticles on the inside of the outer lip, a character not known in other species included in the genus (PONDER, 1985*b*), although VERDUIN (1988) notes that they may be weak or absent in some specimens. Most of the characters that I (PONDER, 1985*b*) used to diagnose the genus *Peringiella* are based on *Peringiella nitida* auct. [= *P. elegans* (Locard)] and the species that I called *P. balteata* (Manzoni). Neither of these species were known previously anatomically. It is shown below that the former species is related to *Cingula* and the latter must be removed from the Rissoidae and is assigned to a new genus in the Hydrobiidae. The status of the genus *Peringiella* remains uncertain.

VERDUIN (1988) reviewed the European species of *Peringiella* and included in the genus *Cingula (Peringiella) eburnea* Nordsieck, 1968. I have examined the type material of this species and it is almost certainly a species of *Hydrobia* as VERDUIN (1988 : 20) also suspected.

The convergence demonstrated by the two species occurring at Ceuta is remarkable. The shells (including their protoconchs) are almost identical (compare fig. 6A, B, G, H with 6E, F, C, D), except in size, as are the opercula (compare fig. 5E and F). The radulae (compare fig. 5A, D and B, C) are also very similar, differing mainly in the slightly smaller number of cusps on the central and lateral teeth and possession of a second pair of basal denticles on the central teeth in *P. elegans*.

« **Peringiella** » **elegans** (Locard, 1892)
(Figs 5A, D, E, 6C-F)

The shell (fig. 6E, F), protoconch (fig. 6C, D), radula (fig. 5A, D) and operculum (fig. 5E) are illustrated for comparison with those of the species discussed below which has previously been considered to be congeneric. The shell (both protoconch and teleoconch) is smooth, about 1.7-2.3 mm in length and 0.8-1.0 mm in width, and has a very thin periostracum. The head-foot (fig. 7A, B) is unpigmented, with a few small, translucent spots behind the eyes and, in some specimens, a few, scattered dense-white spots on the parallel-sided, inconspicuously-ciliated cephalic tentacles (*ct*). The pink buccal mass is visible through the short, prominently bilobed snout. The large metapodial tentacle (*mt*) is broad, with a blunt tip and there is a small posterior pallial tentacle (*pt*). A conspicuous fold on the right side (*nl*) of the neck and a weak fold on the left side (neck lobes of PONDER, 1988) are present. There is a large anterior pedal mucous gland (*apg*) and a posterior pedal gland (*ppg*) with a small, inconspicuous opening (*pgo*; confirmed in sections).

The stomach is rather short, the style sac slightly more than one third to nearly one half
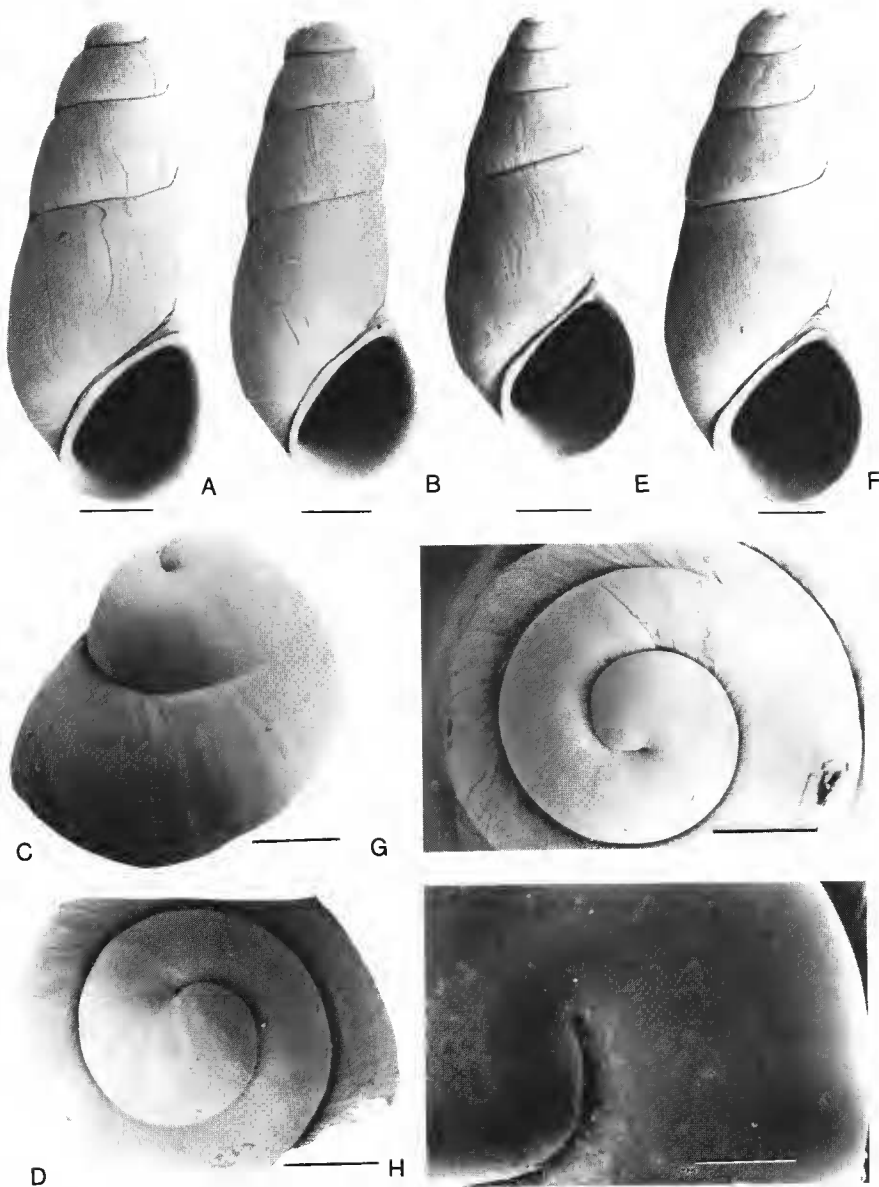
FIG. 6. — A, B, G, H, *Botryphallus epidauricus* (Brusina), shell (A, B) and protoconch (G, H). E, F, C, D, *Peringiella elegans* (Locard), shell (E, F) and protoconch (C, D).
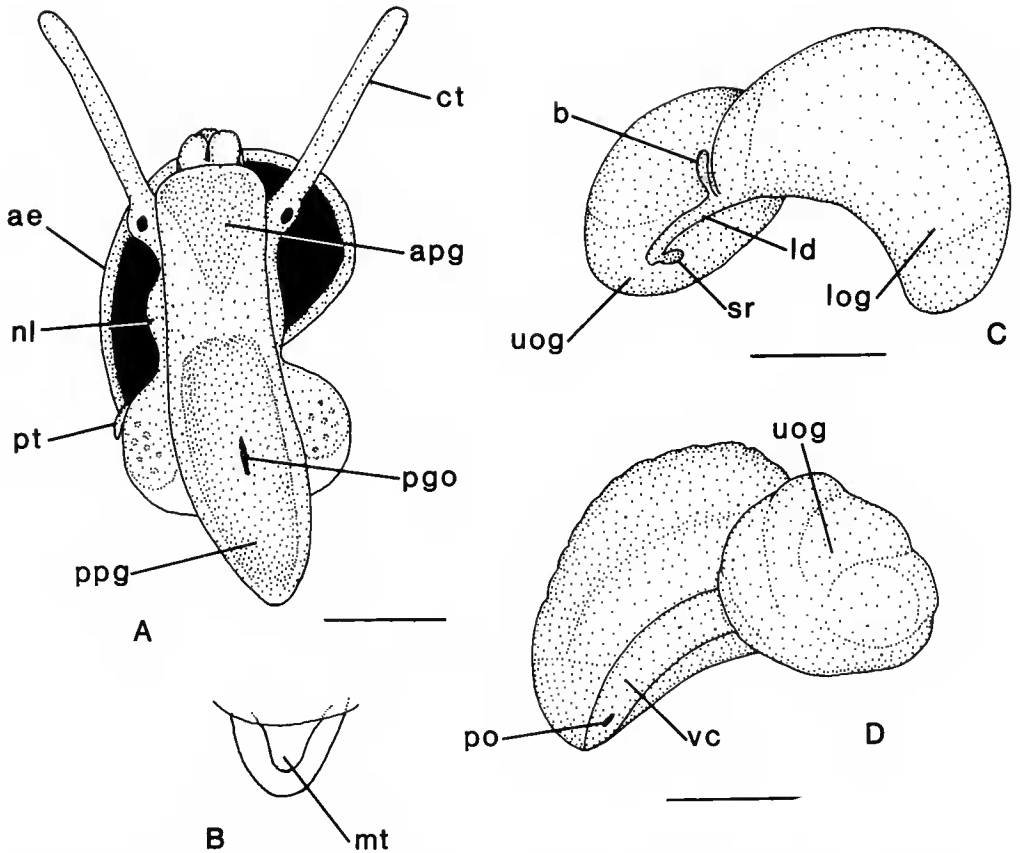Scales : A, B = 0.2 mm; E, F = 0.3 mm; D, C, G = 0.1 mm; H = 30 μm.

FIG. 7. — *Peringiella elegans* (Locard) : A, ventral view of living animal; B, dorsal side of posterior part of foot; C, D, lower part of female genital system from the right (C) and left (D) sides.

ae : aperture edge; *apg* : anterior pedal gland; *b* : bursa; *ct* : cephalic tentacle; *ld* : thin-walled duct between upper and lower oviduct glands; *log* : lower oviduct gland; *mt* : metapodial tentacle; *nl* : right neck lobe; *pgo* : opening of posterior pedal gland; *ppg* : posterior pedal gland; *po* : pallial genital opening; *pt* : pallial tentacle; *sr* : seminal receptacle; *uog* : upper oviduct gland; *vc* : ventral channel of lower oviduct gland.

Scales : A = 0.4 mm; C, D = 0.2 mm.

of the total length of the stomach and open to the intestine along all but the posterior part. The stomachs of living specimens contained foraminiferans (Discorbidae and *Brizalina*).

The seminal vesicle is a twisted, swollen duct on the inner side of the stomach and narrows just behind the posterior pallial wall to become a narrow, ciliated, weakly-muscular duct, the pallial vas deferens, which passes to the base of the penis. At the posterior end of the pallial cavity a very short duct communicates with the pallial cavity. There is no prostate gland. The penis is simple, parallel-sided for most of its length, the distal end tapering to a blunt tip. The penial duct is narrow, straight and enclosed.

The glandular part of the female genital tract (fig. 7C, D) consists of a large lower oviduct gland (*log*) and a globular upper oviduct gland (*uog*) made up of a tightly coiled tubular gland. The lower oviduct gland opens to a thin-walled ventral channel which opens subterminally as a small pallial opening (*po*). Between the two glands on the right side is a small, thin walled bursa copulatrix (*b*) containing unorientated sperm and lined with a thin cuboidal epithelium. This arises from the first part of the ventral duct from the lower oviduct gland which then becomes an elongate duct (*ld*) which passes dorsally and is pressed into the right, antero-ventral part of the upper oviduct gland. At the posterior end of this duct there is a small seminal receptacle (*sr*).

REMARKS

Although this species is tentatively retained in *Peringiella* the head-foot and anatomy of *P. elegans* closely resemble those of the genus *Cingula* (see PONDER, 1985*b*). The final status of *Peringiella* will have to await anatomical details of the type species. VERDUIN (1988) has expressed doubt as to whether this species is congeneric with *P. denticulata*. He has also reviewed this species and gives the distribution as the western part of the Mediterranean, Adriatic Sea and Sicily. VERDUIN also notes the existence of two forms of this species, a slender one and a broad one. The Ceuta specimens belong to the slender form.

VAN AARTSEN *et al.* (1984) and VERDUIN (1988) use the name *Rissoa* (*Cingula*) *nitida* Bucquoy, Dautzenberg and Dollfus, 1884, for this species which is, however, preoccupied so that the name *Cingula elegans* Locard, 1892, should be used as pointed out by PONDER (1985). They do not take this latter course because of potential secondary homonymy with *Rissoa elegans* Grateloup, 1838, and *R. elegans* A. Adams, 1851. The former species appears to be a *Rissoina* and the latter, from the Philippines, is probably an iravadiid, although the type(s) has not been examined. There is thus no chance of *C. elegans* being a secondary homonym of either species.

Family? HYDROBIIDAE

BOTRYPHALLUS new genus

TYPE SPECIES : *Cingula epidaurica* Brusina, 1866.

ETYMOLOGY : *Botryos* (Greek, masc.), cluster of bunch of grapes; *phallos* (Greek, masc.), penis.

DIAGNOSIS

Shell minute, coiled, smooth, tall-spired, with pyriform aperture and dome-shaped protoconch. Operculum thin, simple, with eccentric nucleus. No posterior mucous gland, metapodial or pallial tentacles. Ctenidium reduced, osphradium large. Radula taenioglossate, with single pair of basal cusps, long lateral processes and several rather long, sharp cusps on all teeth. Midoesophagus with long, straight dorsal folds. Stomach without posterior caecum, with single digestive gland opening and short style sac. Rectum lined with large subcuboidal cells with pale-staining contents. Penis with numerous apocrine glands around edges; attached

behind right eye. Prostate gland large, pallial, open by way of a short slit or closed. Female with weakly muscular coiled oviduct, a posterior seminal receptacle and an anterior bursa copulatrix. Bursal duct arises from anterior end of ventral channel. Ventral channel open to lumen of pallial oviduct along entire length. Oviduct gland uniformly staining throughout except for a small anterior area around pallial opening. Both male and female genital glands lined with simple columnar cells.

The taxonomic position of *Botryphallus* is uncertain and it is only tentatively included in the Hydrobiidae. Some of the more discordant characters seen in the new genus are contrasted with other truncatelloidean families below.

Botryphallus epidauricus (Brusina, 1866)
(Figs 5B, C, F, 6A, B, G, H, 8)

The shell (fig. 6A, B) is minute (1.2-1.4 mm in length, 0.55-0.6 mm in width), white, smooth, elongate conical, with about three very slightly convex whorls. The protoconch (fig. 6G, H) consists of about 1.5 dome-shaped whorls which are smooth except for a few extremely weak, minute axial wrinkles. The aperture is ovate, slightly angled posteriorly, the peristome simple. The operculum (fig. 5F) is thin, corneous, simple and has an eccentric nucleus.

The head-foot (fig. 8A, B) is translucent white, the cephalic tentacles (*ct*) long, very slightly tapering distally but the distal end is expanded very slightly and weakly ciliated. The eyes lie at the bases of the tentacles in weak bulges and are surrounded by a few dense white spots. There are no pallial tentacles or metapodial tentacles present. The snout is distinctly bilobed, the distal lobes rather thin laterally and constantly applied to the substratum in life. The snout is about half the length of the cephalic tentacles and the pale pink buccal mass shows through. The foot (fig. 8B) has a well developed, triangular anterior pedal gland (*apg*) and numerous subepithelial glands internal to the sole epithelium. These can be seen through the sole in living specimens and are mainly located laterally. No posterior pedal gland is present. The thin opercular lobes are translucent.

The pallial cavity is long and contains a reduced ctenidium with about 12 small knob-like filaments which extend from the posterior left corner of the pallial cavity to a little behind the mantle edge on the left side of the cavity. The rather large osphradium is broadly oval and reaches from the posterior end of the ctenidium to slightly more than half of the length of the ctenidium. There is a thick hypobranchial gland in the posterior part of the cavity. The pericardium and renal organ do not protrude into the pallial roof, the latter having a well-developed renal gland on its external wall.

The jaws and buccal mass/odontophore are well-developed and typical of the Truncatelloidea. The radula (fig. 5B, C) is taenioglossan, with the central teeth having a strongly concave dorsal edge and the cutting edge bearing (3-)4 + 1 + 4(-3) sharp cusps. The central teeth also have a prominent pair of basal denticles and long, simple lateral processes. The lateral teeth have 3 + 1 + 5 cusps and a long outer shaft. The marginal teeth bear numerous small, sharp cusps confined to their distal ends. The salivary glands pass over the cerebral ganglia. The midœsophagus has long, straight, dorsal folds reaching almost to the irregular, non-glandular ventral epithelium. The stomach has a single digestive gland opening and a short style sac which is about 0.25 the length of the rest of the stomach. The anterior and posterior chambers are subequal, not very distinctly separated externally and no posterior
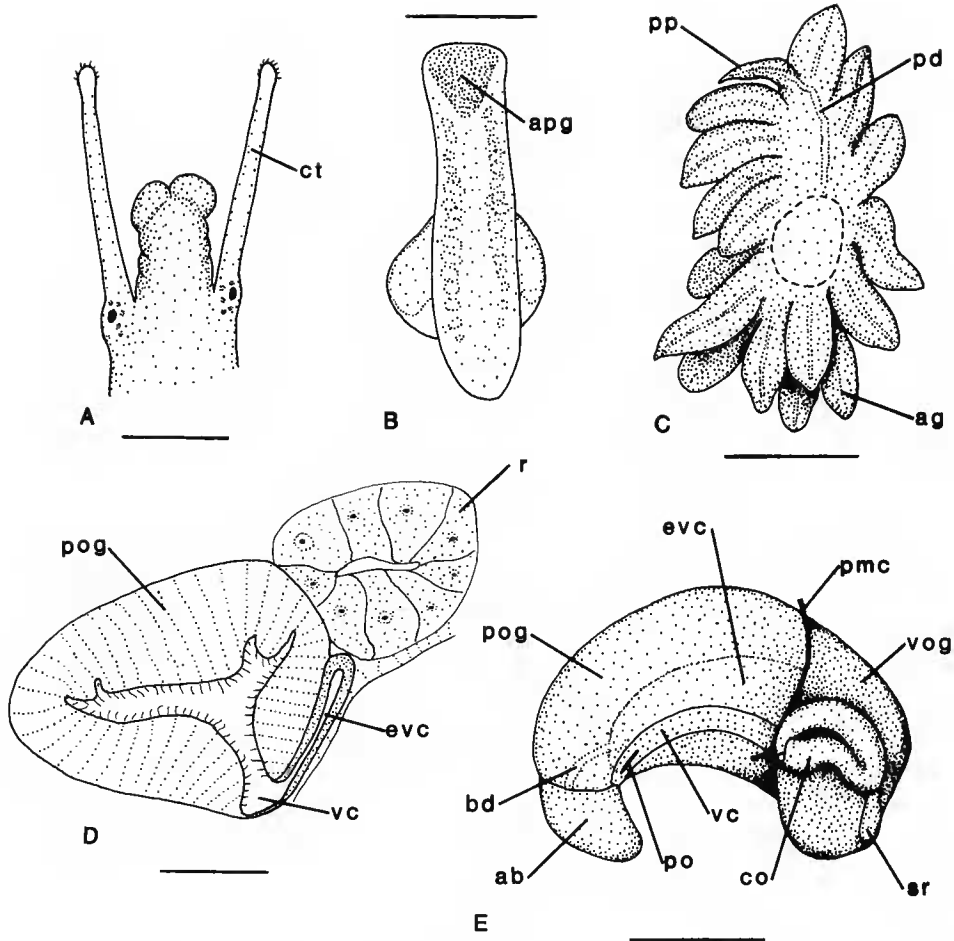
FIG. 8. — *Botryphallus epidauricus* (Brusina) : A, dorsal view of head ; B, ventral view of foot ; C, penis (dorsal view), the dashed line represents the ventral point of attachment ; D, transverse section through the middle part of the pallial oviduct gland and the rectum ; E, lower part of female genital system, viewed from the left side.

ab : anterior bursa ; *ag* : apocrine gland of penis ; *apg* : anterior pedal gland ; *bd* : bursal duct ; *co* : coiled oviduct ; *ct* : cephalic tentacle ; *evc* : dorsal extension of ventral channel ; *pd* : penial duct ; *pmc* : posterior pallial wall ; *po* : pallial genital opening ; *pog* : pallial glandular oviduct ; *pp* : penial papilla ; *r* : rectum ; *sr* : seminal receptacle ; *vc* : ventral channel of lower oviduct gland ; *vog* : visceral glandular oviduct.

Scales : A = 0.2 mm ; B = 0.5 mm ; C, D = 0.1 mm ; E = 0.15 mm.

caecum is present. A semi-liquid crystalline style occupies the style sac and protrudes into the stomach. The rectum (fig. 8D ; *r*) has unusual epithelium consisting of large, subcuboidal pinkish-grey staining cells with finely granular cytoplasm and bearing very short cilia.

The male genital system is dominated by a very unusual, large penis (fig. 8C) which has 15-18 (usually 16) apocrine glands (*ag*) arranged in a single row on both sides and in a double row around the base of the penis. Each apocrine gland has about 6-9 gland cells in any transverse section, these having coarsely granular, red-staining contents and discharge into a

narrow central lumen. The penial duct is more-or-less straight, and discharges through a small, tapering papilla (*pp*). The penis is attached behind the right eye, the point of attachment appearing to be near the middle of the penis because of the cluster of apocrine glands posterior to the attachment area. The pallial vas deferens is simple and enters the anterior end of the prostate gland. The prostate gland is triangular, the broad base abutting against, and protruding slightly into, the posterior wall of the pallial cavity. It is lined with simple columnar gland cells with coarsely granular, red-staining contents and are especially dense in their basal part. These cells open to a narrow, tubular lumen. The visceral part of the vas deferens forms a convoluted seminal vesicle.

The ovary contains a few very large eggs (relative to the size of the animal; up to about 0.3 mm in length and 0.2 mm in diam. in sections). The upper oviduct is non ciliated and lined with pavement epithelium. The lower part of the female genital system is illustrated in figure 8E. The upper oviduct opens to the coiled oviduct (*co*) alongside the posterior part of the albumen gland. The coiled oviduct forms a U-shaped loop and has a silvery appearance because sperm are stored in it. It is lined with a cuboidal epithelium which has numerous long cilia which maintain the sperm in a central rope, and its outer walls are weakly muscular. A rather small seminal receptacle (*sr*) opens to the coiled oviduct at the end of the U, and lies pressed against the posterior wall of the oviduct gland. Sperm have their heads attached to the pavement epithelium lining the seminal receptacle. There is no posterior bursa copulatrix. The coiled oviduct opens to the posterior part of the short, broad, pallial oviduct gland (*pog*). This gland is triangular in shape, almost as wide as long, with the pallial part (*pog*) forming the apex of the triangle, a short, broad posterior section (*vog*) bulging back into the viscera and displacing the renal organ. This posterior section is not curved back on itself like the albumen gland of typical Littoridininae. The pallial opening (*po*) is located near the anterior end of the oviduct gland. The gland is lined with a simple epithelium of dark blue-staining columnar gland cells containing large granules and basal nuclei. In the vicinity of the pallial opening the oviduct gland is lined with ciliated and glandular cells with non-staining contents (mucus?) but otherwise the epithelium appears to be rather uniform throughout (i.e. there is no clear division into an anterior capsule and a posterior albumen gland). Long cilia are present in the oviduct gland and these appear to arise from very narrow cells, with elongate nuclei, wedged between the gland cells. The thin-walled ventral channel (*vc*) is displaced to the left (fig. 8D, E; *evc*) and is lined with small cuboidal, ciliated cells. It continues to the pallial opening after which a short, ciliated tube (*bd*) buds off from its upper surface (the displaced part) and this opens to an anterior bursa copulatrix (*ab*). The anterior bursa is an ovoid pocket which lies anterior to the capsule gland. It is lined with rather short, irregular columnar cells with cytoplasm containing granules and tiny vacuoles.

The large cerebral ganglia abut one another and posteriorly, the pleural ganglia. The right pleural ganglion gives off a connective (about equal in length to the width of the pleural ganglion) to the suboesophageal ganglion. This ganglion lies close to the supraoesophageal ganglion which, in turn, abuts the left pleural ganglion.

REMARKS

The anatomy of *Botryphallus* does not conform with any known family. The apocrine penial glands are otherwise known only in the Caecidae (MARUS & MARCUS, 1963) and

Hydrobiidae (Littoridininae) (THOMPSON, 1968; HERSHLER, 1985; HERSHLER & LONGLEY, 1986; DAVIS & McKEE, 1989). As far as is known all hydrobiids have a posterior bursa copulatrix (except in a few cases where it is lost) and a complex histology of the glandular genital ducts (PONDER, 1988). The caecids have an uncoiled shell, a circular, multispiral operculum, long stationary cilia on the cephalic tentacles and ciliated ridges on the left tentacle. They also lack a coiled oviduct and differ in protoconch morphology. The caecids do, however, share the simple histology of the genital glands and an anterior bursa copulatrix with *Botryphallus*. *Botryphallus* differs from most truncatelloideans in having a semi-liquid crystalline style but MORTON (1975) has recorded a similar style in *Caecum digitulum* (Hedley, 1904). The Elachisinidae (PONDER, 1985*a*) have a penis bearing simple glands and have an open prostate unlike that in *Botryphallus epidauricus*. The female system differs in that the origin of the bursa is from the posterior part of the ventral channel and the albumen and capsule glands are clearly differentiated and stain differently. In addition the histology of the genital glands is of the complex type and the head-foot bears a pair of pallial tentacles and a metapodial tentacle. The penial glands seen in *Botryphallus* are unknown in any Rissoidae and the new genus also lacks an upper oviduct gland, a diagnostic feature of that family. The only other families known to possess a simple histology of the genital glands are the Barleeidae, Anabathridae and Emblandidae. The last family has a very distinctive radula that has no resemblance to the generalised truncatelloidean radula of *Botryphallus*. The Anabathridae have unusual two-layered opercula and simple coiled penes. The Barleeidae have thick, pegged opercula. Both families have posterior bursae.

The Iravadiidae include at least one species with penial glands which resemble apocrine glands (*Iravadia (Fairbankia) australis* (Hedley); PONDER, 1984, fig. 8D). In addition several members of this diverse family have anterior bursae. They differ from *Botryphallus* in all investigated species lacking a coiled oviduct and in all having complex histology of the genital glands.

Botryphallus clearly does not fit comfortably into any of the present family concepts. It is tentatively included in the Hydrobiidae for the following reasons : — the coiled oviduct from which arises a seminal receptacle; shell and radular morphology not discordant; anterior pallial genital opening; general internal and external anatomy. Discordant features include : — the simple histology of the genital glands and the anterior bursa copulatrix. The presence of apocrine glands on the penis would place this genus in the Littoridininae but all other members of that subfamily have the ventral channel stripped away from the pallial oviduct to form a separate tube or a posterior opening and the free end of the albumen gland is twisted anteriorly. One species of *Stygopyrgus* (HERSHLER & LONGLEY, 1986) has a "seminal receptacle" derived from the middle part of the "spermathecal duct" and has lost the posterior bursa copulatrix. It is not known what the histology of the genital glands is in this species; possibly the simple type of histology can occur in such minute species. Clearly elucidation of the taxonomic position of this enigmatic genus will have to await further comparative anatomical studies.

I have not been able to personally confirm the conspecificity of BRUSINA's (1866) species which was described from Dalmatia. This has, however been done by Serge GOFAS who kindly examined some of BRUSINA's topotypic specimens (but not the types) from the Zagreb Museum and provided me with drawings. He concludes that they are conspecific with Ceuta material. VERDUIN (1988) had supposed syntypes available to him and considered material

from the Strait of Gibraltar (near Algeciras) to be the same species. In view of the above considerations I am regarding the Ceuta material as conspecific with *Cingula epidaurica*.

Four specimens (2 of each sex) of another species of *Botryphallus* from the Azores (mid littoral, Island of São Miguel, —/7/1988, collected by S. GOFAS; voucher specimens in MNHN and AMS) to be described by S. GOFAS, have been examined. The anatomy of this species closely resembles that of *B. epidauricus* but the penis has more apocrine glands (19-22) and the anterior bursa is more elongate.

The shell and radula of what may possibly be a third species have been figured by PONDER (1985*b*, fig. 118F, G) as *Peringiella balteata* (Manzoni) from the Canary Islands. VERDUIN (1988) regards this name as a synonym of *B. epidauricus*.

II — INTERTIDAL DISTRIBUTION

Because of the limitations of the sampling technique (see Methods), especially the lack of replicates at each sampling site, little other than gross patterns can be discussed. The consistently low numbers in stn 6 of transect 2 compared with the corresponding stn in transect 1 are probably the result of unavoidable washing of this sample during its collection under water. This sampling problem also applies, although to a lesser extent, to stns 4-6 in transect 1 and stn 4 in transect 2 as these were all collected under water because of the state of the tide and the limited time available.

Skenea serpuloides was in low numbers or absent on the middle shore. Stn 4 on transect 1 (collected underwater and therefore probably partly washed) had a zero count, whereas the corresponding stn on transect 2 had low numbers (14). Low numbers were also recorded in stns 5 and 6 (< 18). It was absent from the middle shore (stns 2, 3) in transect 2 but in low numbers (1, 12 respectively), in transect 1. No specimens were found in stn 1 on either transect.

This species thus appears to live in the interstitial gravel habitat on the lower and, sometimes, middle shore, in low numbers. It was also collected in the sublittoral at Ceuta (S. GOFAS, *in lit.*).

Dikoleps pruinosa had a similar distribution to the last species but achieved higher numbers. In transect 1 it penetrated up the shore to stn 3 (3 individuals) and had increasing numbers down the shore reaching a maximum number at stn 6 (167 individuals). In the second transect it was absent in stns 1-3 but represented by a moderately high number (127) in stn 4 and fewer (25) in stn 6 (probably reflecting greater washing of that sample during collection).

This species appears to be a lower littoral species that penetrates the interstitial gravels only on the lower shore. It was also collected in the sublittoral at Ceuta (S. GOFAS, *in lit.*).

Juveniles of *Gibbula racketti* were abundant on the lower shore (stn 4-6, up to 240 individuals) in both transects, with rather low numbers (< 30) in stn 3, absent (transect 2) or rare (3 individuals) in stn 2 and absent from stn 1.

Caecum incomptum was abundant on the lower middle shore and penetrates the upper middle shore. The highest counts were achieved in stn 4 in both transects (657 and 355

respectively), with numbers dropping considerably in stns 5-6 (transect 1, stn 5 : 120, stn 6 : 53; transect 2, stn 6 : 5). Stn 3 had 551 individuals in transect 1 and only 18 in the second transect. It penetrated further up the shore in transect 1 (to stn 2 with 190 individuals), this stn having a zero count in transect 2. It was absent from stn 1 in both transects.

Caecum clarkii overlapped with the previous species but was not as abundant. Unlike the previous species it appears to prefer the lower shore, with low (2, 3 and 17 respectively in transect 1, stns 2-4) to zero counts (transect 2) in stns 2-3. Stns 5 and 6 in transect 1 and 4 and 6 in transect 2 had rather high numbers (maximum 142, stn 6, transect 1 and 145 stn 4, transect 2).

Peringiella elegans reached the upper middle shore (stn 2) in both transects where it was represented by very small numbers (4 and 1 individuals respectively). It was common in stns 3-6 in transect 1 (104, 211, 89 and 121) and 4 and 6 in transect 2 (225 and 23), the maximum numbers in stn 4 in both transects (211 and 225 respectively). Stn 3 on transect 2 had only 6 individuals. The moderately high numbers from the two lowest samples in transect 1 contrast with the considerably lower number from the lowest station in transect 2, once again suggesting that washing of this latter sample in particular markedly affected the results.

This species, like *Skenea serpuloides, Dikoleps pruinosa, Caecum clarkii* and juvenile *Gibbula racketti*, appears to prefer the lower shore but is capable of penetrating the middle shore when conditions are favourable.

Botryphallus epidauricus is unique in this fauna in having an upper and middle shore distribution. It was the only species found in the uppermost station on both transects (46 and 283 individuals respectively). It achieved very high numbers in stn 3 in transect 1 and stn 2 in transect 2 (1035 and 2152 respectively) making it by far the most abundant gastropod in this fauna. The other upper and middle shore stations also had rather high numbers (stn 2, transect 1 : 220; stn 3, transect 2 : 522). The lower shore stations, by way of contrast, had very low numbers (stns 5, 6, transect 1 : 8, 2; stn 6, transect 2 : 0), whereas station 4 had rather high to moderate numbers (transect 1 : 324, transect 2 : 40).

The abundance of this species in the middle and upper shore and the contrasting very low numbers on the lower shore strongly suggest that it is an intertidal, upper shore species. This species, on the counts available, can reach densities exceeding half a million individuals per cubic metre, more than three times the maximum density of the next most abundant species, *C. incomptum* (538,000 per m^3, compared with 164,250 per m^3).

DISCUSSION

The existence of a fauna of shelled micro-gastropods living interstitially in gravel in the intertidal does not appear to have been reported previously. Faunas associated with boulder beaches of mostly somewhat larger species have been described (e.g. MORTON, 1975) and are indeed not uncommon (pers. observ.). In the same area gastropods such as *Cingula trifasciata*

(J. Adams) are common beneath larger boulders in shaded, more stable areas. *Caecum* has been previously reported from coarse sediments in the littoral (e. g. MORTON, 1975; RISER, 1984). Tiny opisthobranchs are a well known constituent of the interstitial fauna of sandy shores and, in New Zealand (CLIMO, 1980) and S.E. Australia (PONDER, unpublished), the unusual pulmonate slug *Smeagol* lives on shingle beaches in the upper littoral. Ellobiids, assimineids and planaxids are often found in the upper littoral in gravel and boulders. These animals, however, are specialists in upper shore living whereas the Ceuta fauna is distinctly marine, most of the species also being found in the lower littoral and at least two in the sublittoral. A brief general description of the infralittoral pebble "biocenosis" is given by PÉRÈS (1967) and PÉRÈS and PICARD (1964).

The Ceuta fauna is dominated by seven species, one of which is present as juveniles only. An interesting aspect of the fauna is that the six adult species fall into three taxonomic groupings and these species pairs are surprisingly similar in body size and/or general morphology. The two skeneids are similar in size but differ somewhat in shell shape; the two caecids are almost indistinguishable except for the differences in the septum and the two species previously referred to *Peringiella* are very similar, although differing in size. Each of the shell forms in the three groups is very different suggesting that body size is a more important morphological constraint in this habitat than shell shape.

The Ceuta interstitial microgastropod fauna is dominated by *Botryphallus epidauricus* and this species and, perhaps, *Caecum incomptum*, are the only species that appear to be restricted to the intertidal. The others are commonest in the lowermost littoral and presumably shallow sublittoral but penetrate the beach to about the midlittoral level. *Botryphallus* and *Caecum incomptum* appear to prefer different zones on the shore, numbers of the former peaking higher on the shore than *C. incomptum* and *Botryphallus* is also the only species that lives in the upper littoral.

Botryphallus and *Peringiella* were also found at Benzu, on the north west side of Ceuta, in the same habitat as at Sarchal Bay and, presumably, the same fauna will be found at other localities in the Strait of Gibraltar. The same species recorded here in the gravel fauna were found in beach drift by VAN AARTSEN *et al.* (1984) from the Bay of Algeciras, on the northern side of the Strait of Gibraltar. Many of the apparently ideal locations in Ceuta were, however, coated with thick oil deposits which soaked deep into the gravels, especially in the upper littoral.

It is clear that the seemingly inhospitable habitat of a pebble beach is capable of supporting a diverse micromollusc fauna. These habitats, long neglected by biologists, clearly deserve much closer attention.

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